Breeding ecology and phenology of two stream breeding myobatrachid frogs *(Mixophyes fleayi and M. fasciolatus)* in south-east Queensland

Danial S Stratford[1], Gordon C Grigg[2], Hamish I McCallum[3] and Harry B Hines[4]

[1] Centre for Innovative Conservation Strategies, School of Environment, Griffith University, Gold Coast Campus, Qld, 4072.

[2] School of Biological Sciences, University of Queensland, Qld, 4072.

[3] Griffith School of Environment, Griffith University, Nathan Campus, Qld, 4111.

[4] Threatened Species Branch, Environmental Protection Agency, PO Box 64, Bellbowrie, Qld, 4070.
Email: Danial.Stratford@student.griffith.edu.au

ABSTRACT

The breeding ecology and phenology of two sympatric stream breeding myobatrachid frogs were studied across a breeding season in a stream at Cunningham's Gap, south-east Queensland. *Mixophyes fleayi* is listed as endangered and *M. fasciolatus* is considered not threatened. The two species occur sympatrically and their breeding seasons overlap, but they prefer different habitats for breeding and are markedly different in their reproductive ecology. Males of *M. fleayi* formed dense chorusing aggregations in shallow stony riffles of their rainforest stream. The number of individuals comprising the chorus was highly variable and related significantly to ambient temperature and stream height which, with rainfall, humidity and wind intensity accounted for 96.9% of the variation. Male *M. fasciolatus* did not show similar aggregation and called from more dispersed locations. The number of *M. fasciolatus* sighted on any given night showed no correlation with any of the assessed environmental variables.

Mixophyes fleayi appeared to have particular and specialised environmental and habitat requirements for breeding whereas *M. fasciolatus* appeared to be more of a generalist in its reproductive requirements. These differences afforded an opportunity to explore how a species' behavioural and ecological traits may provide resilience to population declines due to climate or habitat alterations.

Key words: Amphibian, *Mixophyes*, endangered, breeding ecology, environmental response, chorus behaviour, oviposition.

Introduction

Declines of amphibian populations have been reported globally, many without a clearly recognised cause (e.g. Kiesecker *et al*. 2001; Stuart *et al*. 2004). Many factors have been examined, including habitat destruction, pollution, introduced predators and competitors, disease and climate change (Kiesecker *et al.* 2001; Hero *et al.* 2005; Skerratt *et al.* 2007; Laurance 2008). Although some of the declines can be explained by these effects, other species have declined in the apparent absence of these factors. A particular puzzle is why some species are declining and not others, even among closely related species. Hero *et al.* (2005) found that among 24 Australian phylogenetic groups examined, eight groups contained both declining and non-declining species.

Ecological studies of population decline often examine causal factors such as global warming, disease or habitat modification, but it is often difficult to explain why some species are strongly affected and others are not. The current study examines and compares some ecological and behavioural traits in two sympatric species of *Mixophyes*, one of which has declined and is considered threatened and one which is apparently stable and is not considered to be threatened (Hines *et al*. 2006a; Hines *et al*. 2006b). The two species, *Mixophyes fleayi* (Fig. 1) and *M. fasciolatus* (Fig. 2) (Anura, Myobatrachidae), have similar morphology and similar breeding periods and clutch sizes (Meyer *et al.* 2001; Morrison 2001; O'Reilly and Hines 2002; Parris

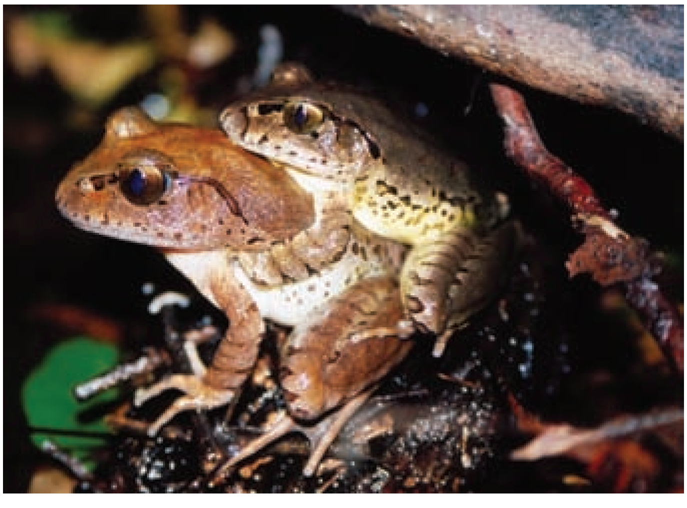

Figure 1. Amplectant pair of *Mixophyes fleayi* on debris in the riffle section of West Gap Creek. Photo: D. Stratford.

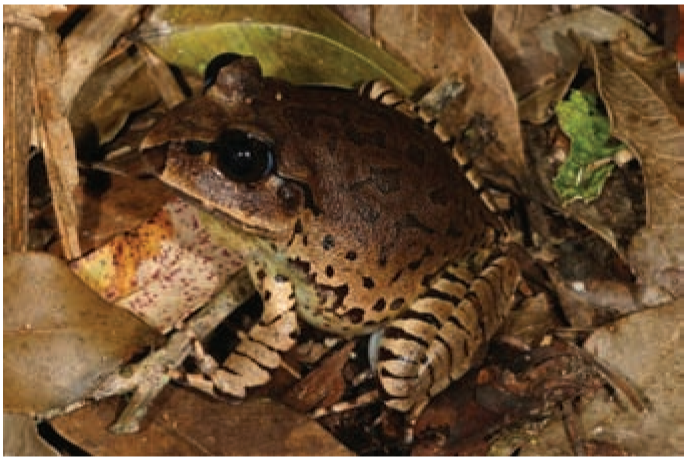

Figure 2. An adult *Mixophyes fasciolatus* near the stream at Cunninghams Gap. Photo: H. Hines.

2002). They provide an interesting comparison between a threatened and non-threatened species, with different life history strategies, habitat specialisation and breeding behaviours, and they offer an opportunity to suggest attributes that may provide resistance to population fluctuations (Hines *et al.* 1999; Bielby *et al.* 2006).

Two sympatric species

Mixophyes fleayi, (Corben and Ingram 1987), occurs in a restricted area of montane rainforest and adjoining wet sclerophyll forests from the Conondale Range in south-east Queensland to the Richmond Range in northern New South Wales (Corben and Ingram 1987; Barker *et al.* 1995; Hines *et al.* 1999). Males can often be found calling from rock or debris perches in or adjoining the stream, as well as from under leaf litter near the stream (Corben and Ingram 1987; Barker *et al.* 1995; Meyer *et al.* 2001). Chorusing aggregations form during suitable conditions from July to March, with previously recognised peaks in activity in October and November and again in February and March (O'Reilly and Hines 2002). Egg deposition occurs in the shallow riffles of streams and tadpoles commonly over-winter (Meyer *et al.* 2001; Anstis 2002). Habitat degradation due to feral animals, weed invasion, changes in flow regimes caused by land clearing and the identification of the fungal disease, chytridiomycosis in the species, are considered possible or contributing causes for population declines (Berger *et al.* 1998; Hines *et al.* 1999). Because of this, and their small and fragmented populations, M. *fleayi* is considered an endangered species under Queensland, New South Wales and federal legislation and in the IUCN Red List.

Mixophyes fasciolatus (Günther 1864), can be found from the Clarke Range in mid-east Queensland to the Gosford area in New South Wales (Hines *et al.* 1999; Parris 2002) in rainforest, wet sclerophyll forest and also in dry sclerophyll forest throughout its range (Parris 2002). This species often breeds in association with streams but, in contrast to M. *fleayi*, it can be found also in association with suitable sized lentic bodies of water, such as dams and ponds (Hines *et al.* 1999; Parris 2002). *Mixophyes fasciolatus* is often found calling from within dense ground cover, under dirt and leaf debris or close from the edge of a clearing, such as path or rock surface (DSS unpubl. data). Breeding is recognised to occur from November to March (Parris 2002) and eggs are deposited on rocks, logs or banks overhanging water bodies (Barker *et al.* 1995; Meyer *et al.* 2001). This species is considered not threatened (Hines *et al.* 2006b).

The IUCN-The World Conservation Union Global Amphibian Assessment conservatively found that 32.5% of amphibian species are currently threatened (Stuart *et al.* 2004). With the expected effects of climate change, ongoing anthropogenic habitat disturbance and the catastrophic effects of disease epidemics, many more species are under real threat of future population reductions and extinction (Berger *et al.* 1998; Stuart *et al.* 2004; Thomas *et al.* 2004; Norris 2007). Knowledge about what attributes make species more or less resilient to habitat change may assist researchers and managers to increase the effectiveness of conservation programs by channelling resources in the most effective way (Field *et al.* 2007).

Methods

Study sites

Two study sites were chosen along West Gap Creek (28° 3' S 152° 23' E) in Main Range National Park, 116 km south-west of Brisbane, Queensland, Australia. The two species breed in different habitats within a kilometre or two of this same creek. The two sites are separated by approximately 2.5 km and are noticeably different in vegetation structure and floral composition. Transects along the stream were established at each study site; the upstream transect was 70 metres long, the downstream transect 50 metres. To determine the density of the breeding aggregations, each transect encompassed only the known or likely oviposition sites for the target species. For the purposes of recording the location of individuals and describing habitat features, transects were divided into 5m sections, each assigned to one of three habitat structure categories (stony riffle, rocky run or pool).

The upstream, rainforest site (Fig. 3) was known to have many M. *fleayi*. The stream here flowed through complex

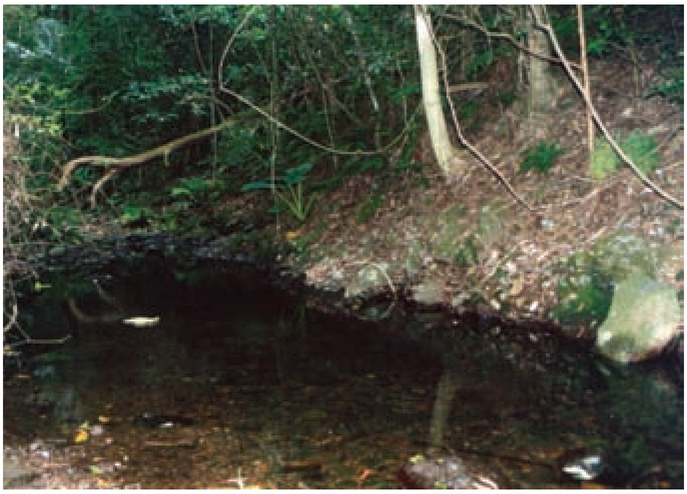

Figure 3. A section of West Gap Creek flowing through the rainforest habitat of Cunninghams Gap. The photo shows the sparse ground level vegetation cover typical of the *M. fleayi* habitat at this site. This section of stream shows an area classified as a pool and is hence not a preferred oviposition site for *M. fleayi.* Photo: D. Stratford.

notophyll vine forest with a closed tree canopy layer and little ground level vegetation. The creek banks comprised exposed soil or leaf litter and, in places, exposed rock. The creek consisted mostly of shallow stony riffles and pools with steep banks in places; the riffle sections of the creek were broad and flat with numerous rounded stones. For extended periods, these areas had a gentle flow of shallow water providing oviposition sites for *M. fleayi* (HBH unpubl. data).

The downstream, open grassy eucalypt forest site (Fig. 4) was known to have numerous *M. fasciolatus.* The creek consisted of a shallowly eroded rock substrate with small cascades and pools. The ground level floristic features of the stream bed and bank were structurally more complex than the upstream site with a dense cover of grasses and mat rush *Lomandra longifolia*, as well as several areas of exposed bedrock. The canopy cover at this site was considerably more open than at the upstream site. Pools, which provide likely oviposition sites for *M. fasciolatus,* were more common than at the upstream site.

Surveys

Fifty-one searches were conducted on the transects between October 2003 and March 2004, 21 at the upstream site, 30 at the downstream site. The October-March period was known to envelop the recognised peak breeding season of both species (O'Reilly and Hines 2002; Parris 2002). Searches were conducted between 19:30 hours and 23:30 hours. Individuals were located by listening for calling males and by spotlighting for eye-shine. Playback or mimicry was not used to elicit vocal responses during the surveys. The presence and abundance of other frog species was recorded also, as were weather conditions, including air and water temperature, stream height, humidity (calculated from wet and dry bulb readings), percent cloud cover, as well as wind and rain intensity (ranked from zero to three). Additionally, temperature and humidity data loggers were placed on both transects, while rainfall was monitored regularly at the Main Range National Park Ranger Station located between the two sites.

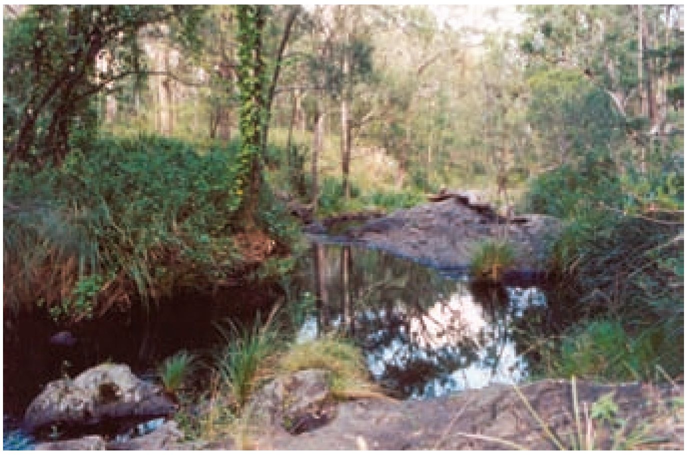

Figure 4. A section of West Gap Creek flowing through the eucalypt forest habitat of Cunninghams Gap. The thick ground level vegetation cover typical of the *M. fasciolatus* habitat at this site can be seen in the photo. The pools and exposed rock are typical along the length of the transect. Photo: D. Stratford.

Data analysis

The influence of abiotic factors on the level of activity of the two species was investigated by regression analysis using R (The Core R Development Team 2003). Correlations were sought between numbers of frogs found and air temperature (at the time of survey), air temperature at 20:00 hours, maximum daily temperature, water temperature at time of survey, humidity, stream height, rainfall (past 24 hours), cumulative rainfall (past 5 days), rainfall two days prior to census, cloud cover and wind intensity. These variables were considered possible or likely to influence activity, based on a knowledge of their breeding biology and because of their known influence on the activities of other breeding amphibians (Blankenhorn 1972; Gooch *et al.* 2006). To reduce problems of collinearity for multiple and stepwise regression, only the temperature and the rainfall variables with the strongest relationship with transect counts were included. Other variables were tested for multicollinearity and fell well below the suggested cut off; $r \geq 0.85$ for collinearity (Knapp 2005). The possible relationship between counts of male and female *M. fleayi* was investigated by correlation, as was the relationship between counts of individuals in each of the species of *Mixophyes* and the total number of species observed on the transect.

Results

Mixophyes fleayi in the upstream rainforest habitat

Twenty-one surveys were conducted in the upstream rainforest transect between 3 October 2003 and 30 March, 2004. Eighty-six percent of surveys revealed either active or calling frogs of at least one of three species, *Lechriodus fletcheri, M. fasciolatus* or *M. fleayi. Mixophyes fleayi* was found in 76% of the surveys, while only one *M. fasciolatus* was recorded here on any night during the study, presumably the same individual. A total of 272 observations were made of either active or calling *M. fleayi* during the surveys. This is likely to include multiple observations of many of the same individuals on different survey nights. However, individuals were counted only once per night. An average of 13 individuals was recorded per night, with a maximum of 38. The number of *M. fleayi* observations made each month is shown in Fig. 5. Males comprised 95% of all individuals observed. The highest number of females recorded was on 9 December 2003 with three individuals. On this evening, the sex ratio was 9:1 with 27 males.

Observations of *M. fleayi* at the stream were highly variable between months (one way analysis of variance: F=9.02; df=5,15; P=0.0004) (Fig. 5). Results of simple linear regressions of counts versus environmental conditions are shown in Table 1. A backwards stepwise regression using minimising Akaike's Information Criterion (AIC) selected temperature at 20:00 hours, stream height and cloud cover as best describing the numbers of *M. fleayi* detected per census (see Table 2). Too few females were observed to model their recorded detections separately from males. However, the number of females observed on any survey night was significantly associated with the number of males detected (r^2=0.524; df=19; P=0.002).

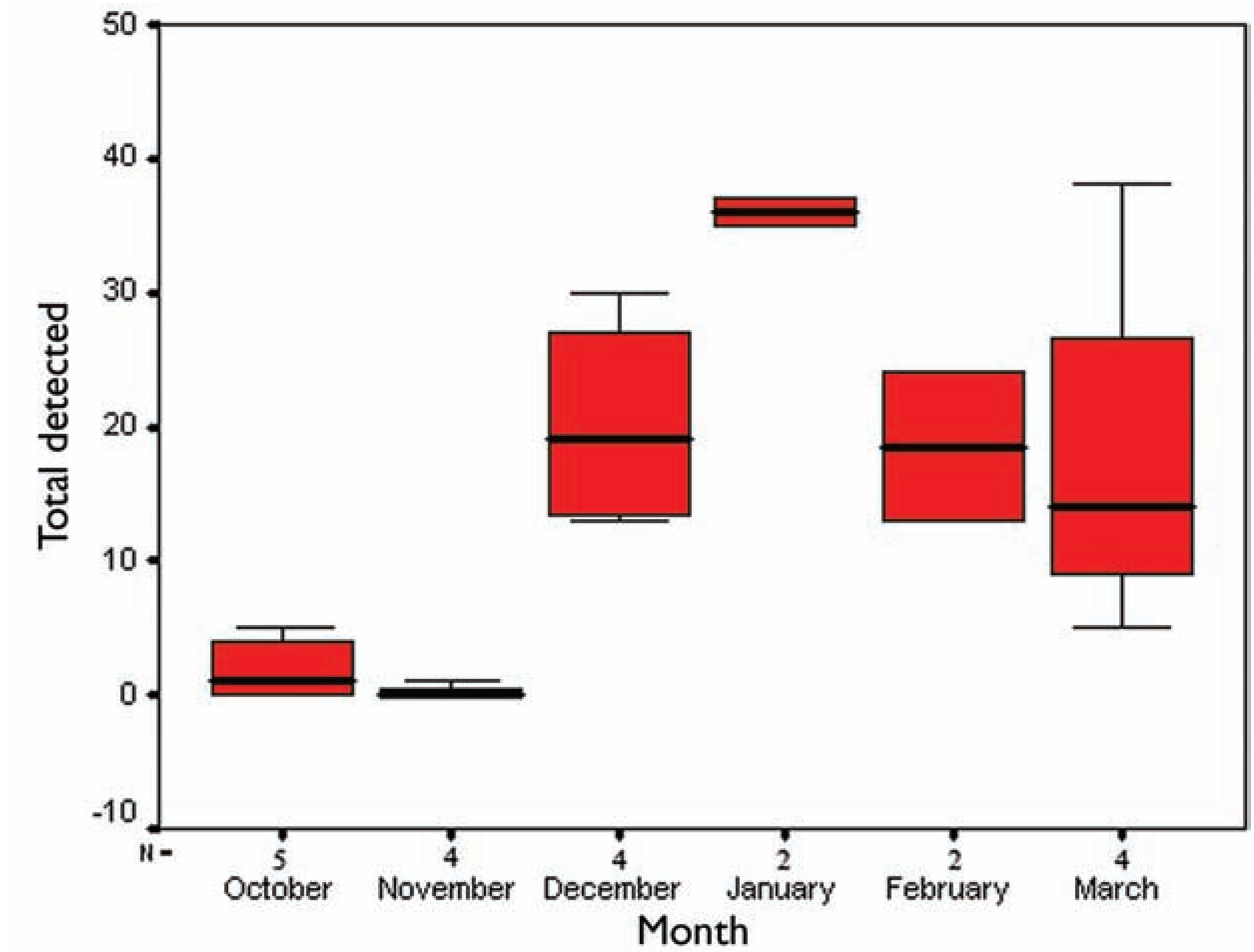

Figure 5. The number of *M. fleayi* found during the 70m transect in each of the survey months (F=9.02; df=5,15; P=0.0004). The box encompasses the interquartile range (i.e. 50% of values), the whiskers extend to the highest and lowest values and the median is indicated by the line across the box. The number of surveys per month is indicated below the horizontal axis.

Table 1. Univariate regressions of *M. fleayi* numbers per survey on environmental variables.

Variable	sign	r^2	d.f.	p
temperature at 20:00hrs	+	0.53	1,18	0.0003
temperature at survey end	+	0.50	1,18	0.0006
stream height	+	0.50	1,17	0.0007
daily maximum temperature	+	0.38	1,18	0.004
water temperature	+	0.29	1,18	0.01
cloud cover	+	0.25	1,17	0.03
Humidity	+	0.14	1,18	0.1
rain (lagged 2 days)	+	0.09	1,18	0.2
rain that day	-	0.08	1,18	0.2
rain (5 day cumulative)	+	0.01	1,19	0.6
Wind	-	0.01	1,18	0.7

The distribution of individuals of *M. fleayi* along the transect was highly aggregated in particular sections of the creek (Fig. 6). A large number of individuals was encountered in some five metre sections (Fig. 7) with few to none in other sections. Similar distribution patterns were observed across the different survey nights, suggesting consistent chorus clustering at particular locations. This consistent distribution allowed for an analysis of substrate preference for this species. Using two-way analysis of variance (structure type crossed with survey date), counts within different sections of the creek were shown to be strongly associated with stream structure (F=16.04; df=2,40; P<0.00001). The areas of the stream that formed deeper pools, cascades or areas of exposed bedrock had significantly fewer individuals than areas of shallow riffles (Fig. 6). The lower numbers and the lack of clustering of individuals of *M. fasciolatus* in a habitat dominated by pools precluded similar analysis.

Mixophyes fasciolatus in the downstream open forest habitat

The open forest habitat with *M. fasciolatus* contained more species of frogs than the rainforest habitat upstream. Ten species were recorded, of which *M. fasciolatus*, *Crinia signifera*, *Litoria pearsoniana* and *Litoria wilcoxii* were encountered most commonly. This habitat contained a greater overall diversity of frog species but *M. fleayi* was absent. In the 30 surveys conducted on this 50m transect between 18 October 2003 and 30 March 2004, *M. fasciolatus* was found to be active in 77.4% of them, with a maximum of 6 individuals detected during any one survey period (mean=2.26). The transect

Table 2. Results of stepwise multiple regression of *M fleayi* numbers per survey on environmental variables.

Variable	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	-40.4115	12.24145	-3.301	0.00573	**
temperature at 20.00hrs	2.45977	0.75012	3.279	0.00598	**
stream height	0.25651	0.08689	2.952	0.01122	*
cloud cover	0.06906	0.04176	1.654	0.12208	
R^2: 0.7916					
F= 16.46; df=3,16; P= 0.0001					

The table shows results of backward selection minimizing AIC applied to a subset of the variables in Table 1 (To reduce collinearity, only the air temperature and rainfall variables with the highest r^2 were used). There is some evidence of a synergistic nonlinear effect of temperature and stream height (P=0.03 for the cross term). Once the above terms are included in the model, no additional variation is explained by the survey month (F=1.36; df=5,8; P=0.33).

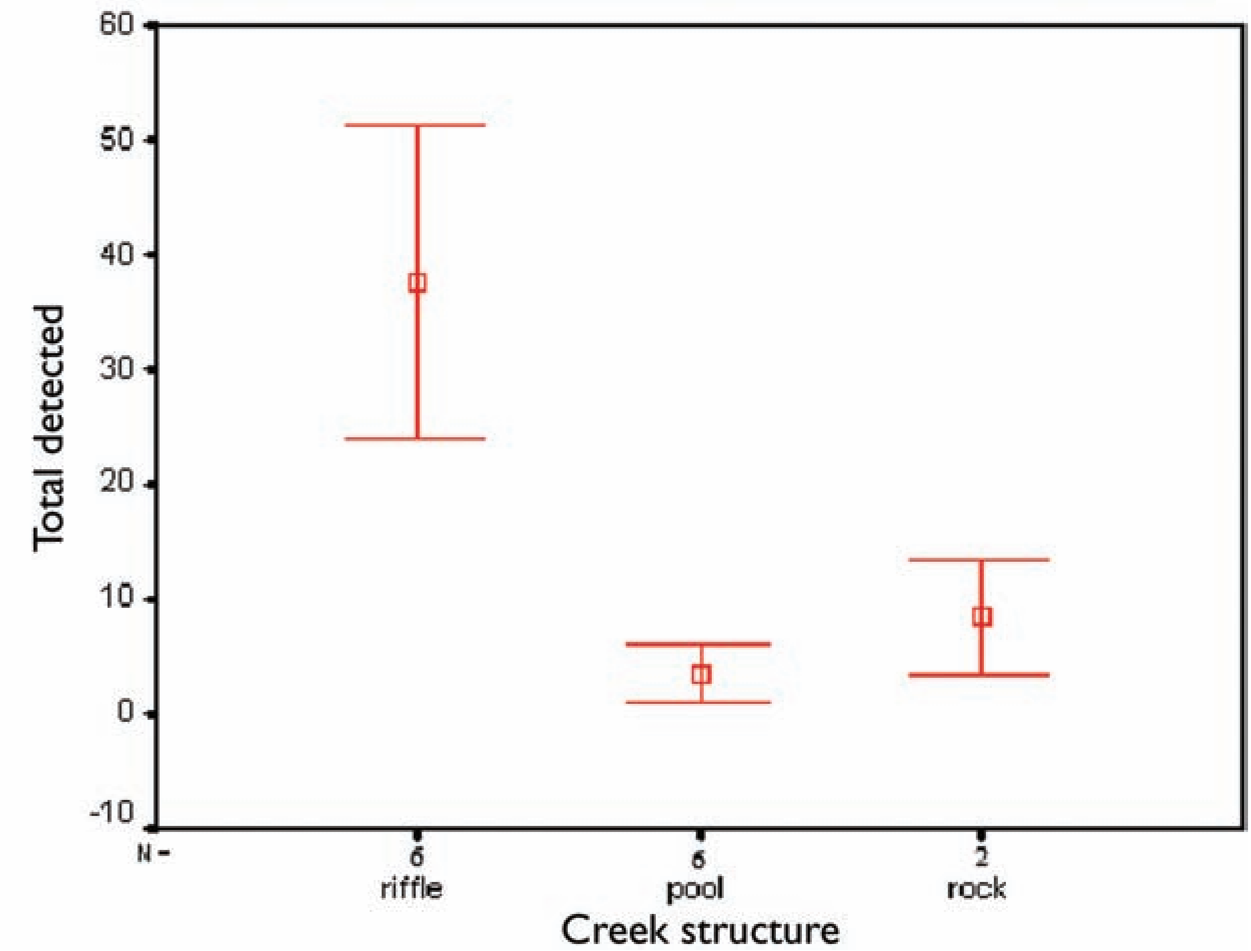

Figure 6. The mean number of *M. fleayi* found within the three different stream structural types (mean of section counts ±2SE) between October 2003 and March 2004. The number of individuals differed significantly between these different stream structural types (F=16.04; df=2,40; P<0.00001, using 2 way ANOVA, structure crossed with survey date). The number of 5m sections per structural type is indicated below the horizontal axis.

counts for the surveys conducted for each month are shown in Fig. 8. Almost all M. *fasciolatus* detected were males, with only one female recorded within the surveys. Unlike M. *fleayi,* aggregations in particular creek sections were not observed. The variance in the number of M. *fasciolatus* recorded per survey (3.45) exceeded its mean (2.19), indicating that the counts did not fit a Poisson distribution (χ^2=47.8; df=30; P=0.02). However, regression analysis revealed no evidence that this heterogeneity in counts was associated with any of the measured environmental factors. The strongest association was with cloud cover (r^2=0.05 (df=27, P=0.2). Further, the average number of M. *fasciolatus* recorded did not vary significantly between months (F=0.76; df=6.27; P=0.6). The best predictor of the number of M. *fasciolatus* observed was the total number of other species found in the transect on that night, although this regression was also weak (r^2=0.11; df=29; P=0.066, but marginally significant for Spearman's test [P=0.04] and Kendall's τ [P=0.019]).

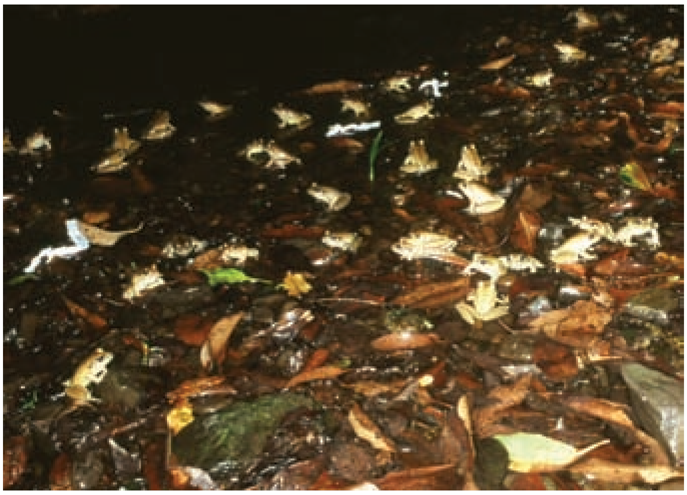

Figure 7. A large number of *M. fleayi* aggregating in a suitable section of the stream. The structure of the stream in which aggregations often formed consisted of riffles flowing through rounded rocks. Photo: H. Hines.

Discussion

Comparative phenology of the two species

The sympatric *M. fleayi* and *M. fasciolatus* are morphologically very similar; however there are large differences in their reproductive behaviour and phenology. During the course of the breeding season, *M. fasciolatus* was observed to display the typical behavioural and phenological attributes of a prolonged breeding species (Wells 1977). Males were found to maintain, on average, relatively steady chorus sizes from October through to March at comparatively low densities, with small and seemingly stochastic variations in the number of observations on the transect (Fig. 8).

In contrast, aggregations of *M. fleayi* formed choruses throughout the survey months, with larger choruses forming between December and March (Fig. 5). Numbers peaked in January, coinciding with the highest recorded monthly rainfall which resulted in a significant increase in stream flow. Temporal activity of *M. fleayi* was highly punctuated, with large variations associated with certain environmental conditions (Table 1); features which are consistent with prolonged episodic breeding strategies (McCauley *et al.* 2000).

Ecology and phenology in reproductive behaviour

In *M. fleayi*, air temperature in combination with stream height was the most significant predictor of numbers of *M. fleayi* observed and the formation of chorus aggregations. This is in agreement with observations reported by O'Reilly and Hines (2002). The response to

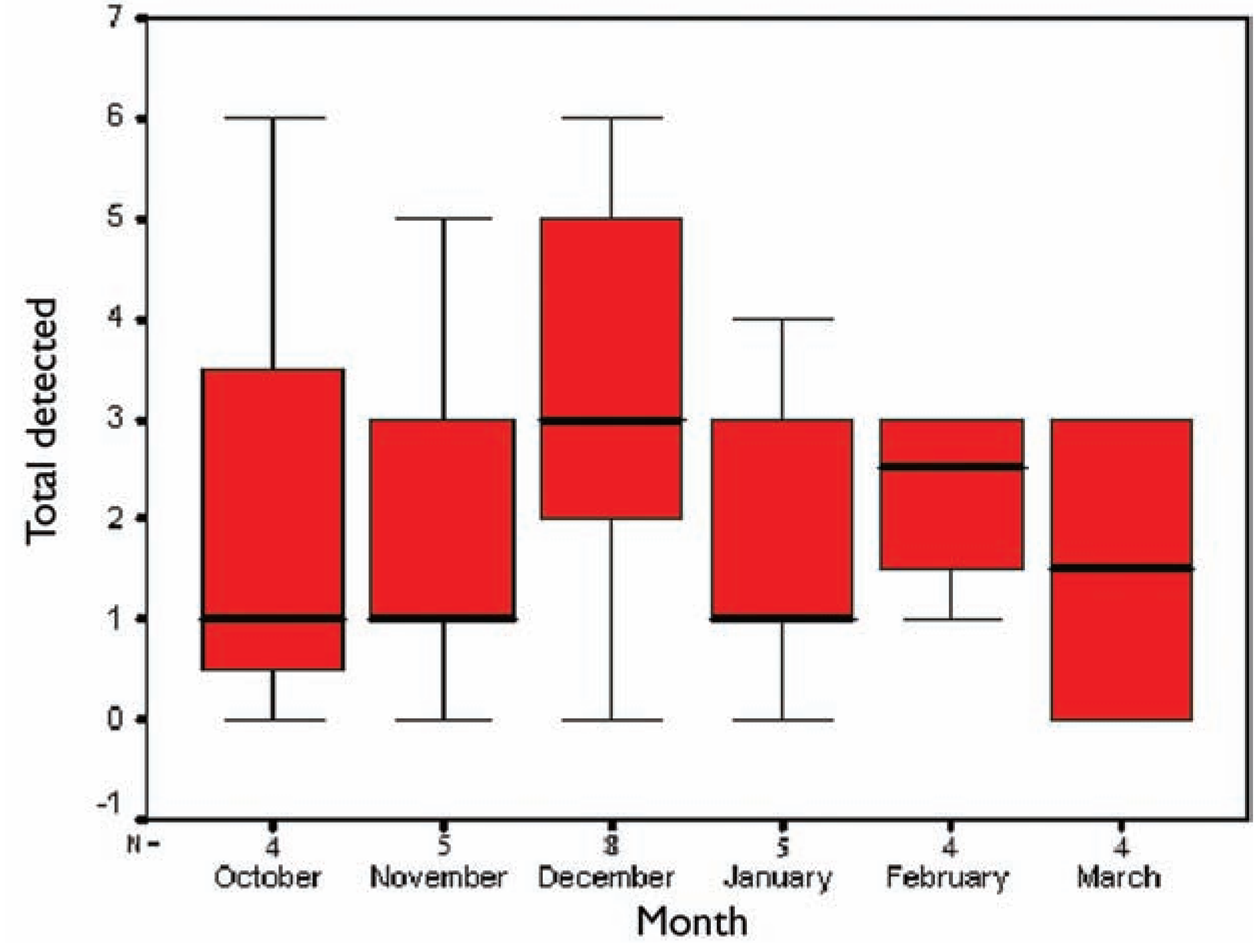

Figure 8. The number of *M. fasciolatus* found along the 50m transect in each of the survey months. There was no evidence that mean counts differed between months (F=0.76; df=6.27; P=0.6). The box encompasses the interquartile range (i.e. 50% of values),, the whiskers extend to the highest and lowest values and the median is indicated by the line across the box. The number of surveys per month is indicated below the horizontal axis.

these two environmental conditions presumably achieves synchronous breeding. These two factors in combination accounted for 68.9% of the variability, and all analysed environmental variables accounted for 96.9% of the variation in numbers detected, suggesting a very strong association between environmental cues or conditions and the formation of chorus aggregations.

In contrast, in *M. fasciolatus,* the number observed on any night showed little association with any of the measured environmental variables. Due to the prolonged breeding season of this species, it is likely that females are less selective of environmental conditions with a greater importance on male quality in reproduction, where male territory ownership, calling tenure and call quality are likely to have a greater selective advantage. In comparison, the stronger dependence of *M. fleayi* on particular environmental conditions results in bursts of breeding behaviour during suitable conditions, resulting in reproductive synchrony.

In species such as *M. fleayi,* the occurrence of cooler conditions is demonstrated to reduce activity related to breeding behaviour (O'Reilly and Hines 2002; Chieffi and Minucci 2004). Due to the costs of reproduction, females, in particular, should be highly selective about when and where oviposition should occur. With the large numbers of males attending chorus aggregations and the high costs associated with egg production, reproductive success in female *M. fleayi* is likely to be limited, not by securing a mate (Fig. 9), but by ensuring survival of the offspring against environmental conditions (Henzi *et al.* 1995; Oseen and Wassersug 2002).

For *M. fleayi,* the number of females detected was strongly correlated with male numbers, with 77.3% of the variance explained. However, whether this is a direct influence, or whether both sexes are responding to the same environmental cues is so far unknown. As the sex ratio remains consistent and very low throughout the season, female activity does not appear to be driven by that of the males, suggesting that males and females are responding to similar environmental triggers and not to each other (Henzi *et al.* 1995). In anurans, sex-biased differential detectability often explains skewed sex ratios, however, ground cover in the rain forest transect was sparse (Fig. 3) and female *M. fleayi* are large frogs with strong eye shine. When they are active at the stream, they are likely to have a similar detectability as males. Thus the low proportion of *M. fleayi* females sighted at the stream per night does not imply a large difference in the population sex ratio, but probably reflects infrequent attendance at the creek by females.

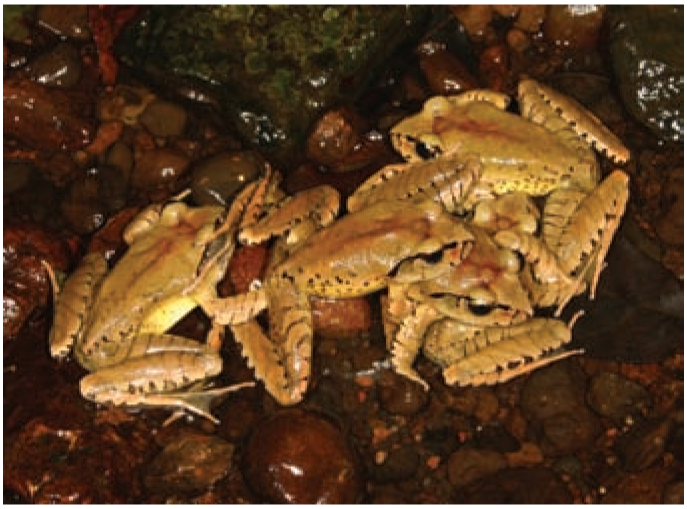

Figure 9. Male competition of *M. fleayi* observed in the riffles of West Gap Creek. No female is present in the photo. Photo by H. Hines.

In order to maximise fitness, males have to offset the risks of predation and energy constraints while maximising reproductive opportunity through sexual advertisement (Brooke *et al.* 2000; Wong *et al.* 2004). On several occasions, rough-scaled snakes, *Tropidechis carinatus* and carpet pythons, *Morelia spilota*, both nocturnal amphibian predators (Shine and Charles 1982; Covacevich and Couper 1992), were observed within the *M. fleayi* choruses. A *T. carinatus* has been seen attempting to ingest an adult female *M. fleayi* at the study site by one of us (HBH). Synchronous breeding aggregations of frogs would provide a good source of food for predators, but aggregation also offers a reduced chance of predation per participating individual (Begon *et al.* 1996; McCauley *et al.* 2000; Bourne *et al.* 2001). This is probably more important for species such as *M. fleayi* where large aggregations form within limited oviposition sites (Fig 9).

A high male sex ratio is typical of a prolonged breeding species such as *M. fasciolatus* (Wells 1977; Crump 1988). In this case however, it is likely to have been exasperated as, although non-calling males were frequently found by eye shine, the transect counts are likely to have underestimated the numbers of females and amplectant pairs due to the difficulty in locating non-calling individuals hidden by dense ground vegetation (Fig. 4). On several occasions, females and amplectant pairs were observed in or around the study area, but not within the transect census periods.

Breeding behaviour and site selectivity

Mixophyes species have large tadpoles, that often take extended periods to complete metamorphosis (Anstis 2002). Tadpoles of these species hence require comparatively large volumes of water per individual to survive to metamorphosis (R. Nattrass, pers. comm.). Due to higher abundances of tadpole predators being found within larger and more permanent water bodies (Hazell *et al.* 2003; Eterovick and Barata 2006), strategies are employed by both these species to reduce the probability of predation during the vulnerable embryonic stage.

Choice of oviposition sites appears highly selective in *M. fleayi,* as calling aggregations of males form within sections of stream having a favourable structure (Fig. 6 & 7), in this case, riffles. The risk of egg predation is believed to apply significant selective pressure on the selection of oviposition sites (Magnusson and Hero 1991; Bourne *et al.* 2001). Eggs of many anuran species have been recorded being eaten by a diverse range of predators, including invertebrates such as insects and leeches, as well as tadpoles and fish (Duellman and Trueb 1986;

Magnusson and Hero 1991; Petranka and Kennedy 1999; Anstis 2002). This effect can be expected to be lower in the shallow riffles where predators such as fish and large tadpoles are restricted.

The selection of areas of riffles during conditions of suitable stream height for oviposition by *M. fleayi* may act as a mechanism to reduce predation of the eggs. However, for this to be successful, both the environmental conditions and the oviposition location must be suitable, if not, they face an increased risk of desiccation with a drop in water level or predation as a result of increased water depth (Merila *et al.* 2004). These considerations illustrate the importance of the selectivity by *M. fleayi* in choosing both a site and a time that will likely ensure suitable stream conditions for larval survival (Henzi *et al.* 1995). *Mixophyes fasciolatus* is known to kick fertilised eggs out of the water to adhere them to a surface above the water level, from which the larvae later wriggle to fall into the water (Meyer *et al.* 2001; Anstis 2002). This has been observed by the authors and includes substrates such as overhanging banks and also low overhanging vegetation. This behaviour is likely to reduce access to the clutch from many aquatic predators, thereby reducing predation. However, the timing of this in *M. fasciolatus* appears to be less dependent upon weather conditions and stream height than in *M. fleayi*.

Conclusion – comparison of life history and breeding strategies

The comparison of these two related species provides an opportunity to examine how the episodic reproductive behaviour and specialised habitat use of *M. fleayi* is indicative of a species with specialised reproductive needs. A combination of both suitable environmental conditions and a suitable site are required for breeding. During occasions or at locations where suitable conditions do not occur, reduced natality may result. This may have detrimental effects on the small populations of this species living in isolated rainforest patches. A specialist species such as *M. fleayi* can be predicted to be more likely to undergo larger population fluctuations than a more generalist species like *M. fasciolatus*, and this may account for its reducing range and smaller population size over recent years, despite it having otherwise similar biological traits.

The broader ecological requirements and the more versatile breeding habits of *M. fasciolatus*, with lower levels of dependence upon specific habitat and environmental conditions are likely to ensure higher likelihoods of successful breeding events (Hines *et al.* 1999; Parris 2002; Bielby *et al.* 2006). Having a larger geographic distribution and habitat range also ensures a higher possibility of metapopulation dynamics buffering against localised declines (Begon *et al.* 1996; Hines *et al.* 1999).

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